NeoBiota 57: 133–152 (2020)
doi: 10.3897/neobiota.57.52195
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Spatiotemporal patterns of non-native terrestrial gastropods in the contiguous United States

Nicholas S. Gladstone[1], Trystan A. Bordeau[2], Christy Leppanen[3], Michael L. McKinney[2]

1 *School of Fisheries, Aquaculture and Aquatic Sciences, Auburn University, Auburn, AL 36849, USA* **2** *Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA* **3** *Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA*

Corresponding author: Nicholas S. Gladstone (nscottgladstone@gmail.com)

Academic editor: Sven Jelaska | Received 18 March 2020 | Accepted 14 May 2020 | Published 17 June 2020

Citation: Gladstone NS, Bordeau TA, Leppanen C, McKinney ML (2020) Spatiotemporal patterns of non-native terrestrial gastropods in the contiguous United States. NeoBiota 57: 133–152. https://doi.org/10.3897/neobiota.57.52195

Abstract

The contiguous United States (CONUS) harbor a significant non-native species diversity. However, spatiotemporal trends of some groups such as terrestrial gastropods (i.e., land snails and slugs) have not been comprehensively considered, and therefore management has been hindered. Here, our aims were to 1.) compile a dataset of all non-native terrestrial gastropod species with CONUS occurrence records, 2.) assess overarching spatiotemporal patterns associated with these records, 3.) describe the continental origin of each species, and 4.) compare climatic associations of each species in their indigenous and introduced CONUS ranges. We compiled a georeferenced dataset of 10,097 records for 22 families, 48 genera, and 69 species, with > 70% of records sourced from the citizen science database iNaturalist. The species *Cornu aspersum* Müller, 1774 was most prevalent with 3,672 records. The majority (> 92%) of records exhibit an indigenous Western European and Mediterranean distribution, with overlap in broad-scale climatic associations between indigenous and CONUS ranges. Records are most dense in urban metropolitan areas, with the highest proportion of records and species richness in the state of California. We show increased prevalence of non-native species through time, largely associated with urbanized areas with high human population density. Moreover, we show strong evidence for a role for analogous climates in dictating geographic fate and pervasiveness between indigenous and CONUS ranges for non-native species.

Keywords

Non-native, land snails, slugs, citizen science, invasive species, data aggregation

Copyright *Nicholas S. Gladstone et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The accidental and deliberate introduction of non-native species is a notable worldwide phenomenon, which has been identified as one of the leading causes of global biodiversity decline (McKinney and Lockwood 1999; Clavero and Garcia-Berthou 2005; Butchart et al. 2010). Moreover, many introduced non-native species are harmful to local and regional economic activities as well as human health (Pimentel et al. 2005; Simberloff 2013; Hulme 2014). The contiguous United States (CONUS; the lower 48 states excluding Alaska and Hawaii) is one of the largest geopolitical areas in the world and contain a diverse array of ecosystems and associated native fauna and flora. Along with many intentional non-native species introductions over several centuries, CONUS has many global transport hubs, facilitating many accidental introductions, and consequently harbors an estimated 50,000 documented non-native species (Pimentel et al. 2005).

Despite much attention devoted to the study of introduced non-native species and their potential impacts in general, some taxonomic groups have received comparatively little study (Pyšek et al. 2008; Jeschke et al. 2012; Lowry et al. 2013). Invertebrate species – primarily insects – comprise a significant proportion of non-native species in the U.S. (US Congress Office of Technology Assessment 1993) and are associated with a myriad of negative impacts on native ecosystems, biodiversity, and economic production (Simberloff et al. 2013; Liebhold et al. 2016). However, the pervasiveness of non-native non-insect invertebrates, such as mollusks, has not been thoroughly studied (Keller et al. 2007; Cowie et al. 2009). Though not all introduced non-native species are directly harmful or later become invasive, monitoring spatiotemporal trends of their presence and spread is useful for management efforts and informs effective policy (Baker and Bode 2016; Mangiante et al. 2018).

Terrestrial gastropods (i.e., land snails and slugs) are generally characterized by low vagility, and they are commonly introduced to new areas from human activities such as the horticultural trade (Cowie et al. 2008; Bergey et al. 2014), non-native pet trade (Cowie and Robinson 2003), use as biocontrol agents (Civeyrel and Simberloff 1996; Cowie 2001), and other cargo shipments (Robinson 1999). Introduced terrestrial gastropods are pests to agriculture and human health and cause significant biodiversity declines in some areas of the world (Cowie et al. 2009; Mazza et al. 2014; Chiba and Cowie 2016; Yeung and Hayes 2018). Broad-scale study of introduced terrestrial gastropods has been primarily limited to dispersal vectors, individual species impacts in specific sites, and risk assessment based on life history traits and invasion history (Robinson 1999; Cowie and Robinson 2003; Cowie et al. 2009). Little study has been given to the geographic fate of these animals when introduced, overarching patterns of presence in their introduced environments, and geographic density through time, all necessary to inform effective policy and management.

Monitoring and study of non-native species can benefit from increasing access to species occurrence data. The Global Biodiversity Information Facility (GBIF; www.gbif.org) and it's U.S. Node, Biodiversity Information Serving Our Nation (BISON;

www.bison.usgs.gov), provide open access databases collectively containing hundreds of millions of occurrence records for species across the tree of life. Other recent efforts focus on digitization of molluscan collections (Shea, Sierwald et al. 2018; Sierwald et al. 2018) and the creation of invertebrate-specific data portals (e.g., InvertEBase, MolluscaBase). There have been criticisms about data quality associated with such large-scale data aggregates (e.g., GBIF) and similar digital resources (Yesson et al. 2007; Troia and McManamay 2016; Bayraktarov et al. 2019) and as such broad-scale analyses of ecology and biogeography may not always be biologically accurate with the data available (Nekola et al. 2019). These limitations considered, these eclectic data resources still allow for numerous evaluations, such as cataloging and estimating the potential pervasiveness of non-native species (e.g., Darrigran et al. 2020). Moreover, compiling all available data for terrestrial gastropods may generate support for additional study and overall improvement of data quality.

Here we describe spatiotemporal patterns of non-native terrestrial gastropods in CONUS. Our aims are to: 1.) compile a dataset of all non-native terrestrial gastropod species with CONUS occurrence records, 2.) assess overarching patterns associated with those records, i.e., spatial and temporal distribution 3.) describe the continental origin of each species, and 4.) compare climatic associations of each species in their indigenous and introduced CONUS ranges.

Methods

Species selection, data collection and contributing sources

To generate our dataset, we first formalized a working definition of the term 'non-native' in the context of our research objectives. We defined non-native terrestrial gastropods as any species that has been either intentionally or accidentally introduced into CONUS and that is indigenous to areas outside of North America. As the geographic distributions of terrestrial gastropod species are generally understudied, native ranges of species documented only outside of CONUS but within North America might indeed include CONUS. Therefore, species that are native to Canada and Mexico are not considered in this study, nor are extralimital species that are native to portions of the U.S. but have been translocated to other regions within the country (e.g., *Euglandina rosea* Férussac, 1821). To identify non-native species' records, we compiled all available information from state and federal governmental technical reports, scientific literature (e.g., Robinson 1999, Cowie et al. 2009), online data aggregators (GBIF, BISON), citizen science databases (iNaturalist), online collection portals specific to museum collections (InvertEBase), online data repositories specific to invasive or pest species (e.g., USDA APHIS, found at www.aphis.usda.gov/aphis/home/), and direct conversation with several malacologists (Robert Cowie, Daniel Dourson, Gerald Dinkins personal communication). Though we are confident in the overall breadth of our search efforts, we also acknowledge that this may represent an incomplete dataset.

Importantly, we also recognize the body of analytical and statistical quandaries associated with data sourced from citizen science networks and other large data aggregators (Bird et al. 2014; Kosmala et al. 2016; Bayraktarov et al. 2019). Our goal was to catalog and outline the potential pervasiveness of these non-native species by synthesizing all available data. Therefore, we note that we did not correct for spatial biases (e.g., spatial autocorrelation), nor did we adjust our data based on possible pseudo-replication, detection rates, or other common sources of geospatial data error. Thus, we encourage readers to treat our results as a synthesized dataset from which they can then begin to adjust for spatial biases for future geospatial modeling (e.g., species distribution modeling).

We utilized the online portal MolluscaBase (available at www.molluscabase.org) to verify the taxonomic identity of all species and to avoid double counting synonymous records. In cases of species being known by several taxonomic identities, searches for each identity were subsequently searched for, placed under the most updated synonym, and records were thoroughly searched by all authors to avoid overlap. When records were identified as erroneous, questionable, or of limited utility (e.g., falling outside CONUS or directly within the centroid of a county), they were removed from the dataset. If a detailed location description was provided for a record that did not contain a georeference, we georeferenced these records using the web application GEOLocate (available at www.geo-locate.org/).

Data were separated into three different sets for reporting: 1.) all records with or without georeferences, 2.) all records with georeferences, and 3.) all records with georeferences and temporal data. The second dataset with all georeferenced records was used for all downstream summaries beyond explicit analyses of spatiotemporal trends, for which the third dataset was used. Lastly, records were categorized by source: 1.) museum and natural history collections, 2.) state or federal governmental agency, 3.) scientific literature that did not already have records associated with a museum collection, and 4.) citizen science database.

Continental origin and climatic associations

Literature and geospatial data pertaining to each species identified as non-native in CONUS were reviewed and used to assign a continental origin with respect to the species' indigenous range. Several species (e.g., *Cornu aspersum* Müller, 1774) were assigned multiple continental origins, as they exhibit intercontinental geographic distributions in their indigenous ranges. In scenarios where continental origin was obscure or unknown, the species was removed from this analysis (i.e., all species in the genus *Allopeas* Baker, 1935, *Gulella* Pfeiffer, 1856, *Laevicaulis* Férussac, 1822, *Opeas* Alber, 1850, and *Subulina* Beck, 1837). To assess climatic associations of each species in its native and CONUS environments, we categorized species by the Köppen-Geiger climate classification system (Rubel et al. 2017). Georeferenced records collected via GBIF and historical literature designating indigenous range were separately gathered

and projected in ArcMap v.10.7 by ESRI. These records were spatially joined with a high resolution Köppen-Geiger climate zone projection (Rubel et al. 2017; available at koeppen-geiger.vu-wien.ac.at/present.htm) and the climate classification was extracted to each individual record. Similarly, we repeated this process for our curated database of comprehensive CONUS records to classify introduced climate association. Many species occupy multiple climate zones and are therefore included in all such occupied zones respective to each species. To visualize these data, the *circlize* package (Gu et al. 2014) was used in R v.3.6.1 (R Core Team). To enhance the interpretability of these visualizations, all classifications that yielded lower than ten observations were removed.

Spatiotemporal trends in the contiguous United States

To assess spatial distribution through time of all non-native species, we projected records on a map of the contiguous U.S. at five time intervals starting from the first georeferenced record: 1862–1940, 1941–1960, 1961–1980, 1981–2000, and 2001–2019. The initial, large interval was used due to sparsity of records from the first georeferenced record until the mid-20th century, followed by a standard two-decade delimitation. To identify areas with many non-native species records, the Point Density tool in ArcMap v.10.7 was used with a circular neighborhood of 75 km at each respective time interval. All time intervals were standardized to a single density scale.

Species richness and number of records in CONUS were quantified by political state boundaries by spatially joining record location data to a polygon layer of the contiguous U.S. Additionally, records were assessed in association to contemporary land cover type and human population density. We used the 2016 National Land Cover Database (NLCD; available at https://www.mrlc.gov/data/nlcd-2016-land-cover-conus) through the U.S. Geological Survey (Yang et al. 2018). Human population density data were obtained through the 2018 U.S. Census from the U.S. Census Bureau (TIGER/Line shapefiles; available at https://www.census.gov/cgi-bin/geo/shapefiles/index.php). The raster files were converted to point data and spatially joined to a polygon layer of 0.5 km buffers created around each record location. Land cover type was consolidated into seven categories: agricultural, barren, developed, forest, herbaceous, shrub/scrub, and wetlands.

Results

Data collection, species occurrences and data sources

From all sources, we assembled a dataset comprising 13,311 records for 25 families, 59 genera and 93 species. Of these records, 10,097 records included georeferences (with 134 records georeferenced by the authors), and 9,297 records included temporal information and georeferences. The full georeferenced dataset was used to generate the

final taxonomic list, containing 22 families, 48 genera and 69 species (see Table 1). The majority of non-native species records are in California (5,735 of 10,097), with 26 of the total 69 species documented represented within the state (Fig. 1). Non-native species richness is more evenly distributed across various states, with all but two states (Nebraska and South Dakota) with at least one non-native species record.

The most prevalent and widespread species documented is *Cornu aspersum*, with nearly three times as many CONUS records (3,672) as the next most prevalent species *Otala lactea*. *Cornu aspersum* records are densely clustered in metropolitan areas along the west coast (incl. California, Oregon and Washington) with many records in south-central Texas, the southern Midwest, and along the eastern seaboard (Fig. 2).

The second most prevalent species, *O. lactea* (1,297 records) exhibits a similarly broad introduced distribution to *C. aspersum*, most commonly associated with coastal areas in the west (California, Oregon) and in the east (Florida). Additional records are clustered within the northeast (Michigan, New York, Vermont). Records of the third and fourth most prevalent species, *Rumina decollata* (998 records) and *Limax maximus* (756), are primarily within metropolitan areas along the west coast (e.g., Los Angeles and San Francisco, CA, Seattle, WA) and in the central U.S. (e.g., Dallas, TX). These major urban hubs appear to be hot spots for introduction of these terrestrial gastropods. The most geographically widespread non-native species was *L. maximus*, being found from coast to coast in 37 of the 48 states.

Of the four contributing source categories to all records, a large majority (7,917 of 10,097 records) are from the citizen science database iNaturalist. Museum and natural history collections contribute 2,131 records, state and federal governmental agencies contribute 24 records, and 25 records come from scientific literature not associated with museum collections.

Continental origins and climatic associations

Europe is the continental origin for the majority of non-native CONUS species identified, with 25 genera and 45 species with a strictly European origin. An additional ten genera and eight species have a broad Mediterranean distribution that encompasses Western Europe and Northern Africa (see Table 1). Proportionally, species indigenous to the aforementioned continental regions collectively make up 92.2% of CONUS records, and the remainder of species with certain origins come from Asia (2.8%), the Caribbean (0.06%), and Central and South America (0.01%) (see Fig. 3). Of the species documented, *Cornu aspersum* records are the most widespread and numerous. This species has a Mediterranean distribution (and was accordingly categorized with both an African and European origin in Fig. 3) but given that the majority of species are being translocated from Europe, we infer that this species may be disproportionately transported from the northern extent of its native range. Thus, the frequency of introduction from northern Africa is likely to be proportionally smaller.

Table 1. Non-native species list curated from the full georeferenced dataset. The 'x' designates genera or species with obscure or unknown continental origins.

Species Name	Number of records	Origin	State Records
Cornu aspersum	3,672	Europe, Africa	AL, AR, AZ, CA, CO, FL, GA, ID, KS, LA, MA, NH, NM, NV, NY, OH, OR, PA, SC, TN, TX, UT, VA, WA
Otala lactea	1,288	Europe, Africa	CA, FL, GA, KY, MO, MS, NM, NY, PA, TX, VA, WV
Rumina decollata	989	Europe, Africa	AL, AZ, CA, FL, GA, LA, MS, NC, NM, OR, PA, SC, TX, WV
Limax maximus	745	Europe	AL, AR, AZ, CA, CO, CT, DC, DE, GA, ID, IL, IN, KS, KY, MA, MD, ME, MI, MO, MT, NC, NJ, NV, NY, OH, OK, OR, PA, SC, TN, TX, UT, VA, VT, WA, WI, WV
Limacus flavus	371	Europe	AL, AR, AZ, CA, DC, FL, IN, KS, LA, MD, MO, MS, NC, NJ, NY, OK, OR, PA, TN, TX, WA, WI
Cepaea nemoralis	317	Europe	CA, CT, ID, IL, KY, MA, ME, MI, MN, MT, NJ, NY, OH, PA, RI, TN, UT, VA, WA, WV
Oxychilus draparnaudi	294	Europe	AL, CA, DE, GA, ID, IL, IN, MA, MI, NC, NJ, NY, OH, OR, PA, SC, TN, TX, VA, VT, WA
Bradybaena similaris	277	Asia	AL, FL, GA, LA, MS, NC, OK, SC, TX, WI, WV
Arion subfuscus	224	Europe	AL, CT, DC, DE, IL, IN, KY, MA, MD, ME, MI, MN, NC, ND, NH, NJ, NY, OH, OR, PA, TX, VA, VT, WA, WI, WV, WY
Milax gagates	185	Europe	AR, CA, DC, OK, OR, TX, VA
Arion rufus	126	Europe	AR, CA, FL, ME, MT, NY, OK, OR, PA, WA
Allopeas gracile	115	x	AL, FL, GA, IL, LA, MO, NC, NJ, OK, PA, SC, TX, VA
Subulina octona	112	x	FL, IL, OK, PA, TN, TX, VA
Theba pisana	105	Europe, Africa	CA, NY, TX
Oxychilus cellarius	95	Europe	CA, IA, IL, IN, MA, MD, ME, MI, NJ, NY, OH, OK, OR, PA, RI, SC, VA, WA
Arion hortensis	85	Europe	CA, CT, DC, DE, IL, KY, MA, ME, NC, NJ, NY, OH, PA, VA, WA, WV
Arion sp.	74	Europe	CT, DE, IA, IL, KY, ME, MI, MN, NC, NH, NY, OR, PA, TN, TX, VA, VT, WA
Opeas pyrgula	72	x	AL, FL, GA, IL, LA, MD, MS, NC, SC, TN, TX, VA, WV
Allopeas micra	71	x	FL, MO, TX
Ambigolimax valentianus	66	Europe	AL, AR, CA, DC, DE, GA, MD, MS, NC, NY, OK, SC, TN, TX, WA
Limax sp.	63	Europe	AL, AZ, CA, CO, IL, KS, KY, LA, MA, MD, MT, NC, NJ, NM, NY, OH, OR, PA, WA, WV
Arion circumscriptus	58	Europe	CA, GA, ID, IN, MA, MD, ME, MI, NC, ND, NY, OK, PA, WI
Xerotricha conspurcata	56	Europe, Africa	CA, WA
Bulimulus guadalupensis	49	Caribbean	FL
Succinea putris	46	Europe	MA, ME, MI, NY, OH, PA, VT
Myosotella myosotis	45	Europe, Africa	CA, FL, NY, OR
Arion fasciatus	41	Europe	CT, IA, IL, IN, MA, MD, ME, MI, MN, NC, NY, PA, TN, WI, WV
Arion intermedius	33	Europe	CA, DC, IL, IN, MA, MD, NJ, NY, OH, OR, VA, WA
Arion ater	26	Europe	MD, MT, NC, NJ, NY, WA
Cernuella cisalpina	25	Europe	MD, NC, NJ, OH, VA
Deroceras agreste	25	Europe	CA, CT, DC, IN, MA, MI, NJ, NM, NY, OR, PA, WA
Gulella bicolor	25	x	FL, SC, TX
Oxychilus sp.	25	Europe	CA, FL, NJ, NY, PA, WA
Massylaea vermiculata	23	Europe, Africa	LA, NJ, NY, OH, PA, TX, WV
Cepaea hortensis	22	Europe	CA, MA, NY, OH, RI, TX
Allopeas clavulinum	21	x	FL, IL, LA, MS, NC, OK, PA, TX
Helix pomatia	18	Europe	CA, FL, MA, MI, NY, PA, WI
Opeas hannense	18	x	FL, GA, IL, LA, MO, NC
Hygromia sp.	17	Europe, Africa	MA, ME
Cochlicella barbara	16	Europe	CA, SC
Oxychilus alliarius	15	Europe	CA, ID, IN, NJ, NY, PA, RI, WA
Lissachatina fulica	12	Africa	FL
Otala punctata	12	Europe, Africa	GA
Cecilioides acicula	9	Europe	CA, IL, PA, TX
Ovachlamys fulgens	9	Asia	FL, IL
Helicella sp.	8	Europe	NC, SC, VA
Lehmannia marginata	8	Europe	CA, IL, MA, ME, MO, OR, TX

Species Name	Number of records	Origin	State Records
Leptinaria sp.	7	South America, Central America, Caribbean	TX
Trochulus hispidus	7	Europe	AL, IL, NJ, NY, VT
Lauria cylindracea	6	Europe	CA
Monacha cartusiana	5	Europe	AL, DE, OH
Veronicella sp.	5	Central America, Carribean	FL, TX
Cepaea sp.	4	Europe	NC, NY
Cernuella virgata	4	Europe	KY, MI, NJ
Milax sp.	4	Europe	OR, TX
Tandonia kusceri	4	Europe	IL
Arion distinctus	3	Europe	OH, WV
Laevicaulis alte	3	x	FL, TX
Tandonia budapestensis	3	Europe	DC, PA
Arion vulgaris	2	Europe	OR
Bradybaena sp.	2	Asia	NC
Helicella elegans	2	Europe	NC, SC
Helicella caperata	2	Europe	NC, VA
Helicella variabilis	2	Europe	NC
Lehmannia sp.	2	Europe	WA, WV
Xerolenta obvia	2	Europe	MT
Xeroplexa intersecta	2	Europe	NC
Allopeas sp.	1	x	FL
Arianta arbustorum	1	Europe	MA
Arion silvaticus	1	Europe	IL
Cochlicella ventricosa	1	Europe	SC
Cochlicella acuta	1	Europe	MI
Cochlodina bidens	1	Europe	NY
Ena obscura	1	Europe	IN
Helicarion sp.	1	Africa	NC
Helicella intersecta	1	Europe	VA
Leptinaria lamellata	1	South America, Central America, Caribbean	FL
Lissachatina immaculata	1	Africa	NM
Megalobulimus oblongus	1	South America, Central America, Caribbean	NY
Neocyclotus sp.	1	Central America, South America	OR
Oxychilus helveticus	1	Europe	CA
Papillifera sp.	1	Europe, Africa	NY
Subulina sp.	1	Europe, Africa	GA
Veronicella cubensis	1	Central America, Caribbean	FL
Xeropicta krynickii	1	Europe, Africa	KY

Climate zone associations in indigenous and CONUS ranges of most species were similar. Of the seven species reported from tropical climate zones in the Caribbean, Central America, or South America, all CONUS records were also associated with tropical or humid subtropical climates (largely found in southern Florida). Likewise, > 97% of CONUS records for the two introduced Asian species come from the same zone as their indigenous environment. All but two species (*Lissachatina fulica* Bowdich, 1822, and *L. immaculata* Lamarck, 1822) with indigenous ranges including Africa are associated with Mediterranean-influenced climates, although most of these species'

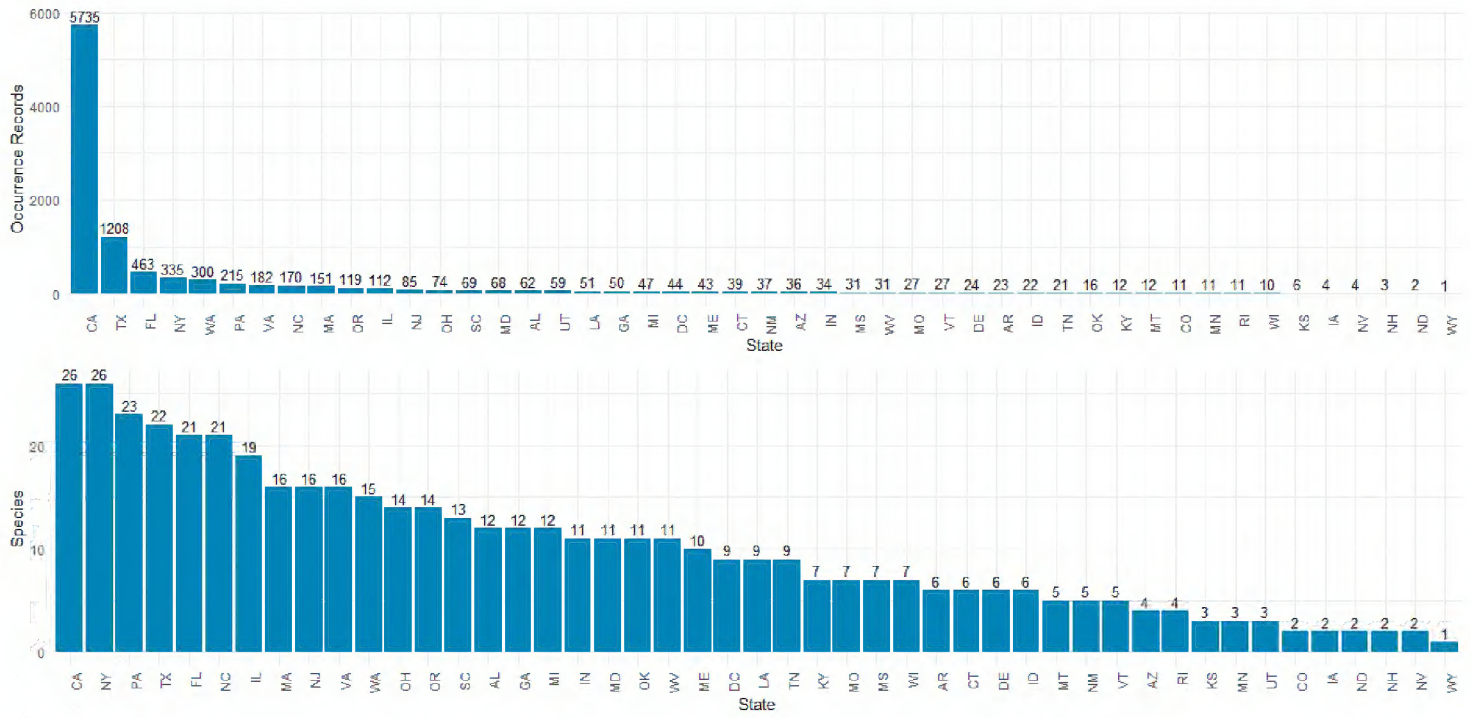

Figure 1. Bar plots of records (**Top**) and species richness (**Bottom**) by CONUS state including the District of Columbia. Nebraska and South Dakota are excluded with zero occurrences in these states.

ranges also include several additional climate zones in Western Europe. As such, both the African and European fauna have a higher diversity of climatic associations in both their indigenous and CONUS ranges. However, there is significant overlap between the broad climate classifications, with the primarily temperate, Mediterranean, and boreal climate zones being the dominant associations for indigenous and CONUS ranges.

Spatiotemporal trends in the contiguous United States

Land cover type associated with records of the non-native species identified is primarily developed (47.2%). Records are largely clustered around areas of high human population density and urban sprawl. Within the three states with the highest number of records (California, Texas, Florida, respectively), areas with rapidly growing recorded density are major cities. For example, 2,819 records are from Los Angeles County alone, which comprises over one fifth of our entire georeferenced dataset. Records not associated with developed land were generally evenly spread across the other major land cover type categories (see Fig. 4).

Few CONUS introductions were discovered from the first record in 1862 until 1940 (see Fig. 5). From then on, the number of records roughly doubled every two decades until 1980. From 1981–2000, the increase in records declined to an estimated 30.8%. Overall, increased record density was primarily associated with eastern coastal states, with gradual extension into the central U.S. However, very likely owing to the advent of digital tools to record species observations (e.g., iNaturalist), in the past two decades there was an estimated 797% increase in non-native species records. Recorded density in the last two decades has been heavily centralized in western coastal states in areas of urban sprawl, as well as in urban hubs in central states such as Texas.

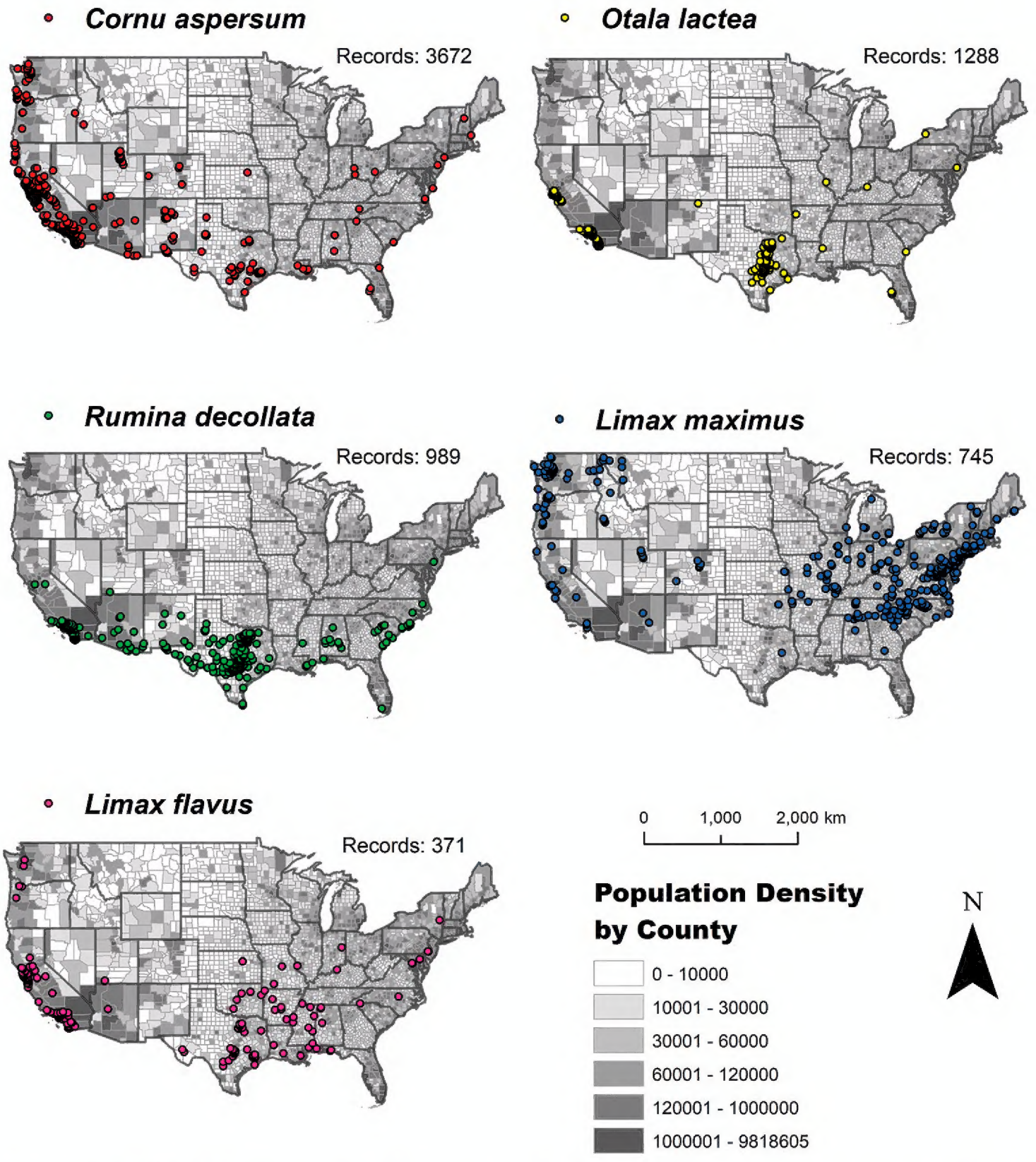

Figure 2. CONUS distribution of the five most prevalent non-native species in relation to county-based U.S. population density.

Discussion

Spatial and climatic mechanisms for species introduction

Our results indicate that hot spots of gastropod introductions occur in highly urbanized areas. This generally conforms to previous findings showing a significant correlation, at several spatial scales, between introduced species diversity and human population size. Examples of this correlation include invasive plants (Campos et al. 2016; Vinogradova

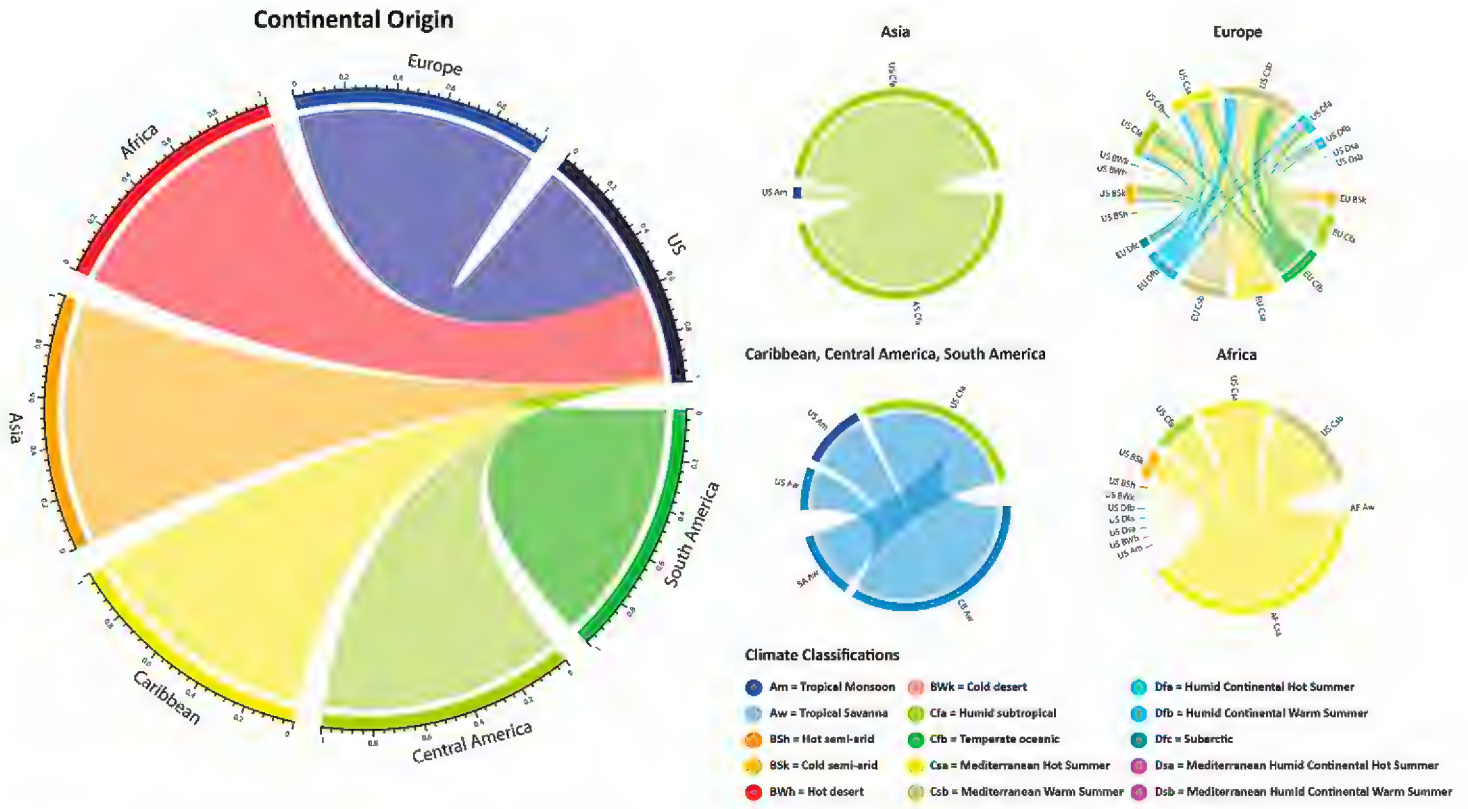

Figure 3. Left: Relative contribution of each continental indigenous origin for non-native CONUS terrestrial gastropod species records. **Right**: Climatic associations of each non-native species in the indigenous range and it's CONUS records utilizing the Köppen-Geiger climate classification scheme. Illustrations are subdivided by continent or a grouping of continents in relative proximity. Color codes are defined for each classification, and the two-letter code preceding each climate code identifies the respective region (AF = Africa, AS = Asia, CA = Central America, CB = Caribbean, EU = Europe, SA = South America, US = United States).

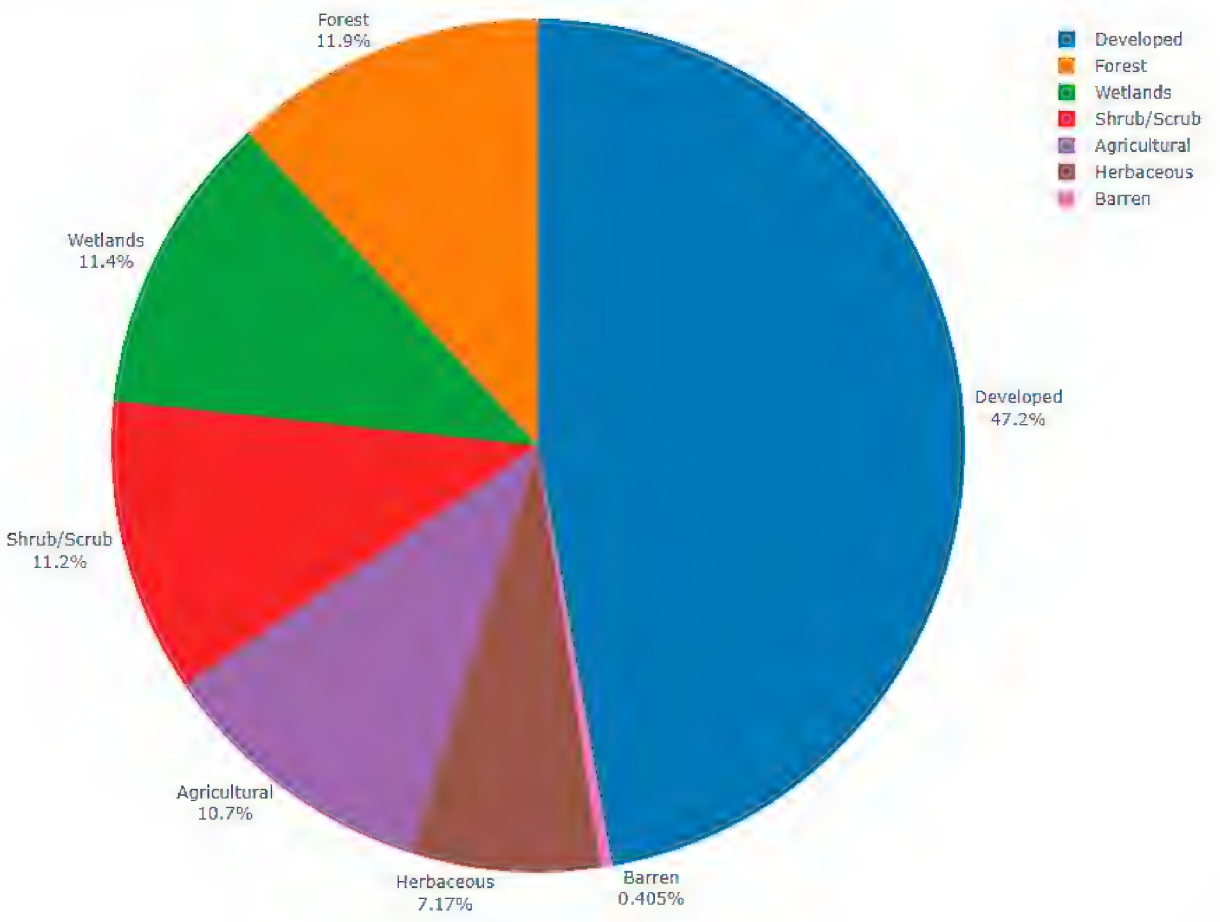

Figure 4. Proportions of 2016 NLCD land cover type in relation to 0.5 km buffer surrounding each record.

et al. 2018) and invasive animals (Spear et al. 2013). One driver of this association is that increasing human population density leads to increased importation (dispersal) of non-native species into an area via intentional and unintentional introductions. More people in an area inevitably leads to more opportunities for introduction of ornamental plants, weeds, pets and many other well-documented pathways of non-native species importation (Pimentel et al. 2005; Simberloff 2013). Another driver of this correlation is that more people in an area produce increased anthropogenic disturbances, altering native habitat which eliminates many native species and creates habitat for non-native species (McKinney 2001). There is also a likely artifactual contribution to this correlation: increasing human population densities create a sampling bias by increasing the likelihood that more species (including introduced and invasive species) will be observed and recorded (Barbosa et al. 2013). This is especially true given the rapid rise of citizen science programs and social media platforms, especially iNaturalist.

The geospatial analyses also show that introduction hot spots tend to occur in highly populated areas concentrated along coastal regions at several latitudes (Fig. 5). Comparable areas of human population density located away from coastal areas tend to have much lower non-native species diversity. This pattern conforms to findings that ports of entry are gateways to many introduced species, especially non-native horticultural plants (Jehlik et al. 2019) and animals such as invasive insects (Langor et al. 2009) and invasive terrestrial gastropods (Bergey et al. 2014) that are hitchhikers on such plants. A key implication is that these organisms might gradually disperse into the interior of the continent, as seen in Fig. 5. This could be accelerated by punctuated dispersal events, e.g., following applicable aforementioned mechanisms, that might also occur.

Our results also suggest that native to introduced range climate analogs are positive factors in non-native terrestrial gastropod diversity and pervasiveness. Most non-native terrestrial gastropod species found in our study are located in climate zones similar to their native ranges, e.g., species primarily of Mediterranean origin recorded in Pacific coastal states in the introduced range. Previous studies have documented evidence of such climate matching in other groups, including invasive fishes (Howeth et al. 2016) and reptiles and amphibians (van Wilgen et al. 2009). A study of European non-native land snails also found evidence of climate matching but with several important exceptions that demonstrated the importance of including (where possible) species traits as an explanatory variable in understanding non-native snail distributions (Capinha et al. 2014).

Non-native species diversity and prevalence

The contiguous U.S. (CONUS) harbors a greater non-native terrestrial gastropod diversity than other New World nations (Naranjo-García and Castillo-Rodríguez 2017; Darrigran et al. 2020). This may be the product of greater interest in malacology within the U.S., as well as the popularity and accessibility of citizen science media. However, there are still notable sampling gaps within the country, and therefore this representation probably underestimates the full taxonomic scope of non-native terrestrial gas-

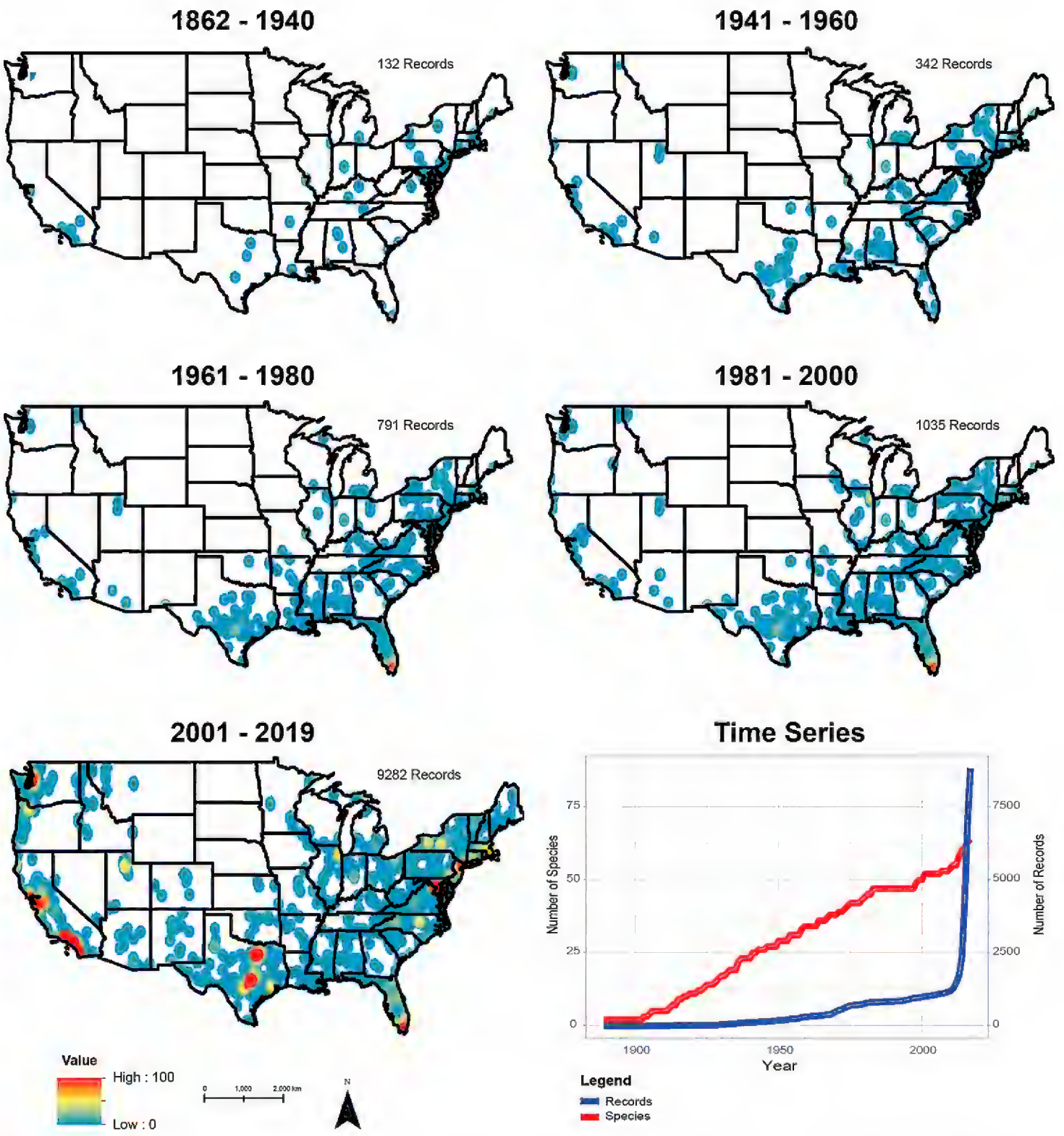

Figure 5. Point density map of non-native species records at five different time intervals. High-density values were associated with 100 or more records within a 75 km circular neighborhood around each individual record. Records were cumulative for each respective interval and tallied on the right side of each map. Time series data associated with new species and records shown in bottom right.

tropods. Our results corroborate findings of Dawson et al. (2017), that the majority of species richness and abundance records were found in predominantly coastal areas. This is also supported by a recent study of non-native mollusks in South America (Darrigran et al. 2020).

Although most non-native terrestrial gastropod species exhibit climate matching to their indigenous ranges (discussed above), there is notable variation in the extent of occurrence and abundance of records between species. While analogous climate conditions might thus promote successful introductions of terrestrial gastropods in CONUS

or other areas, there are clearly other factors driving the success of some non-native species relative to others. Generalist characteristics and broad thermal tolerances might contribute to survivability in a new habitat (McKinney and Lockwood 1999). Also, other life history traits and reproductive strategies in terrestrial gastropods might facilitate establishment from small populations (i.e., hermaphroditism, large clutch sizes; Robinson 1999). For example, there is a substantial literature attributing such traits to *Cornu aspersum*, the most widely recorded species in our dataset (Guiller et al. 2012; Gaitán-Espitia et al. 2013; Nicolai et al. 2013; Nespolo et al. 2014).

The pet and aquarium trade, increasing trade in ornamental and agricultural plants, as well as human food preferences have contributed to the importation and spread of invasive terrestrial gastropods within the contiguous U.S. Though our findings cannot directly quantify the relative importance of each of these dispersal vectors, there are apparent correlations between the geographical abundance of records for particular species and likely mechanisms. For example, *C. aspersum* and *Otala lactea* are among the most common land snail species used in human food consumption (escargot) owing to their fast reproductive rates and high nutritional content (Dragićević and Baltić 2005). These species are found in high densities in major U.S. cities such as San Francisco and Los Angeles, CA, Portland, OR, and Dallas, TX. Increased demand for exotic dishes in such communities, some with high socioeconomic areas, might provide greater opportunity for escape and persistence (i.e., via high propagules pressure) compared with less cosmopolitan areas. Other idiosyncratic drivers of success may be at play when considering the pervasiveness of these non-native species.

Potential impacts in light of spatial patterns

We did not consider impacts of any non-native species in this study, and therefore cannot directly infer potential economic or ecological harm associated with our results. The invasiveness and deleterious impacts of many of these species have been comprehensively reviewed in other literature (e.g., Robinson 1999; Cowie and Robinson 2003; Cowie et al. 2009), and we encourage those interested to seek additional information about these topics elsewhere. Using our data, however, we can provide further utility to previous projections of select non-native species and their negative impacts (if any), specifically those of Cowie et al. (2009). This previous research sought to quantify the potential 'pest significance' of a variety of non-native gastropod species based on life history traits, propagule associations, invasion history, general ecology, and other biological and historical factors. Species considered (both aquatic and terrestrial in this case) were then scored individually and proportionally to all others within their dataset using these factors, with those scoring highest being projected as most ecologically harmful.

Of the non-native terrestrial species considered of high potential risk included in Cowie et al. (2009), we surprisingly note that few have a substantial number of records in our dataset. For example, the genus *Cernuella* was scored individually and propor-

tionally highest among terrestrial groups in Cowie et al. (2009), yet our data collection yields only 29 records of this genus in CONUS associated with two species (Table 1). The most prevalent species in our dataset, *C. aspersum*, was ranked in the lower extent of the top one third of the nearly 50 species considered in Cowie et al. (2009), along with another fairly prevalent species in our dataset (*Theba pisana*). All other species in this top one third of their dataset have fewer than 20 records. We do note, however, that the majority of our records do not have associated estimates of abundance (and thus this was not considered in our study), so few records of any one species should not infer a lack of future ecological harm. Instead, it can be used to inform management efforts in areas with species considered potential pests.

Source contribution

While the spatiotemporal trends exhibited in our dataset are consistent with other studies of non-native taxonomic groups within the U.S. (e.g., Mangiante et al. 2018), it is important to acknowledge limitations in this study and provide caution about its interpretability. Citizen science has become an increasingly popular tool both in terms of scientific analysis and to connect the general populous with the scientific community (Follett and Strezov 2015). So much so, in fact, that it here represents a impressively significant portion of our final dataset. For example, the Los Angeles County Museum of Natural History has initiated a new mollusk-specific citizen science program called *Snails and Slugs Living in Metropolitan Environments* (SLIME; https://nhm.org/community-science-nhm/slime). There have been a number of published products associated with this program (e.g., Ballard et al. 2017; Vendetti et al. 2018), and the vast majority of records in Los Angeles County (and by extension many in our dataset) are a product of participants of this program via iNaturalist. Thus, while these efforts have been successful and prolific, we advise caution when using all data provided for geospatial modeling without first accounting for common sources of geospatial error (e.g., spatial autocorrelation, pseudo-replication).

Conclusion

Our study seems to support a growing interest in the distribution of non-native terrestrial gastropods through time, with rapidly increasing amounts of records being contributed to museum collections and other digital repositories. We believe this trend will grow as citizens grow steadily aware of what non-native species might be in their vicinity, which can be greatly informed by localized science outreach and BioBlitz programs (e.g., Ballard et al. 2017). In conclusion, our results represent the first synthesized geospatial dataset of non-native terrestrial gastropods in CONUS, with over 10,000 individual records spanning over 150 years of collection efforts. A significant biodiversity is represented in our dataset, though the number of records disproportion-

ally indicates the increased prevalence of just a handful of species. We show increased prevalence of non-native species through time, largely associated with urbanized areas with high human population density. Moreover, we show strong evidence for a role for analogous climates in dictating geographic fate and pervasiveness between indigenous and CONUS ranges for non-native species. We believe this study serves as a first step toward a more driven effort to outline future research of these non-native species, including more geospatially-robust predictive distribution modeling, risk assessment, and overall management.

Acknowledgements

We thank I Killius and E Pieper for additional logistical efforts, R Cowie for helpful comments early in the manuscript's conception, and A Simpson for information regarding the use of BISON data.

References

Baker CM, Bode M (2016) Placing invasive species management in a spatiotemporal context. Ecological Applications 26(3): 712–725. https://doi.org/10.1890/15-0095

Ballard HL, Robinson LD, Young AN, Pauly GB, Higgins LM, Johnson RF, Tweddle JC (2017) Contributions to conservation outcomes by natural history museum-led citizen science: examining evidence and next steps. Biological Conservation 208: 87–97. https://doi.org/10.1016/j.biocon.2016.08.040

Barbosa M, Pautasso M, Figueiredo D (2013) Species-people correlations and the need to account for survey effort in biodiversity analyses. Diversity and Distributions 19(9): 1188–1197. https://doi.org/10.1111/ddi.12106

Bayraktarov E, Ehmke G, O'Connor J, Burns EL, Nguyen HA, McRae L, Possingham HP, Lindenmayer FB (2019) Do big unstructured biodiversity data mean more knowledge? Frontiers in Ecology and the Environment 6: 1–239. https://doi.org/10.3389/fevo.2018.00239

Bergey EA, Figueroa LL, Mather CM, Martin RJ, Ray EJ, Kurien JT, Westrop DR, Suriyawong P (2014) Trading in snails: plant nurseries as transport hubs for non-native species. Biological Invasions 16(7): 1441–1451. https://doi.org/10.1007/s10530-013-0581-1

Bird TJ, Bates AE, Lefcheck JS, Hill NA, Thomson RJ, Edgar GJ, Stuart-Smith RD, Wotherspoon S, Krkosek M, Stuart-Smith JF, Pecl GT (2014) Statistical solutions for error and bias in global citizen science datasets. Biological Conservation 173: 144–154. https://doi.org/10.1016/j.biocon.2013.07.037

Butchart SHM, Walpole M, Collen B, Van Strien A, Scharlemann JPW, Almond REA, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE (2010) Global biodiversity: indicators of recent declines. Science 328(5982): 1164–1168. https://doi.org/10.1126/science.1187512

Campos JA, Baquero GG, Cano L, Loidi J, Herrera M (2016) Climate and Human Pressure Constraints Co-Explain Regional Plant Invasion at Different Spatial Scales. PLoS ONE 11(10): e0164629. https://doi.org/10.1371/journal.pone.0164629

Capinha C, Roedder D, Pereira HM, Kappes H (2014) Response of non-native European terrestrial gastropods to novel climates correlates with biogeographical and biological traits. Global Ecology and Biogeography 23(8): 857–866. https://doi.org/10.1111/geb.12176

Chiba S, Cowie RH (2016) Evolution and extinction of land snails on oceanic islands. Annual Review of Ecology, Evolution, and Systematics 47: 123–141. https://doi.org/10.1146/annurev-ecolsys-112414-054331

Civeyrel L, Simberloff D (1996) A tale of two snails: is the cure worse than the disease? Biodiversity & Conservation 5(10): 1231–1252. https://doi.org/10.1007/BF00051574

Cowie RH, Robinson DG (2003) Pathways of introduction of nonindigenous land and freshwater snails and slugs. In: Ruiz G, Carlton JT (Eds) Invasive Species: Vectors and Management Strategies. Island Press, Washington, 93–122.

Cowie RH (2001) Can snails ever be effective and safe biocontrol agents? International Journal of Pest Management 47(1): 23–40. https://doi.org/10.1080/09670870150215577

Cowie RH, Hayes KA, Tran CT, Meyer III WM (2008) The horticultural industry as a vector of alien snails and slugs: widespread invasions in Hawaii. International Journal of Pest Management 54(4): 267–276. https://doi.org/10.1080/09670870802403986

Cowie RH, Dillon RT, Robinson DG, Smith JW (2009) Alien non-marine snails and slugs of priority quarantine importance in the United States: A preliminary risk assessment. American Malacological Bulletin 27(1/2): 113–133. https://doi.org/10.4003/006.027.0210

Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution 20(3): 1–110. https://doi.org/10.1016/j.tree.2005.01.003

Darrigran G, Agudo-Padrón I, Baez P, Belz C, Cardoso F, Carranza A, Collado G, Correoso M, Cuezzo MG, Fabres A, Gutiérrez Gregoric DE, Letelier S, Ludwig S, Mansur MC, Pastorino G, Penchaszadeh P, Peralta C, Rebolledo A, Rumi A, Santos S, Thiengo S, Vidigal T, Damborenea C (2020) Non-native mollusks throughout South America: emergent patterns in an understudied continent. Biological Invasions 22(3): 853–871. https://doi.org/10.1007/s10530-019-02178-4

Dawson W, Moser D, Van Kleunen M, Kreft H, Pergl J, Pyšek P, Weigelt P, Winter M, Lenzner B, Blackburn TM, Dyer EE (2017) Global hotspots and correlates of alien species richness across taxonomic groups. Nature Ecology & Evolution 1(7): p.0186. https://doi.org/10.1038/s41559-017-0186

Dragićević O, Baltić MŽ (2005) Snail meat: significance and consumption. Veterinarski Glasnik, 59(3–4): 463–474. https://doi.org/10.2298/VETGL0504463D

Follett R, Strezov V (2015) An analysis of citizen science based research: usage and publication patterns. PloS ONE 10(11): e0143687. https://doi.org/10.1371/journal.pone.0143687

Gaitán-Espitia JD, Arias MB, Lardies MA, Nespolo RF (2013) Variation in thermal sensitivity and thermal tolerances in an invasive species across a climatic gradient: lessons from the land snail *Cornu aspersum*. PLoS ONE 8(8): e70662. https://doi.org/10.1371/journal.pone.0070662

Gu Z, Gu L, Eils R, Schlesner M, Brors B (2014) *circlize* implements and enhances circular visualization in R. Bioinformatics 30(19): 2811–2812. https://doi.org/10.1093/bioinformatics/btu393

Guiller A, Martin M, Hiraux C, Madec L (2012) Tracing the invasion of the Mediterranean land snail *Cornu aspersum aspersum* becoming an agricultural and garden pest in areas recently introduced. PLoS ONE 7(12): e49674. https://doi.org/10.1371/journal.pone.0049674

Howeth JG, Gantz CA, Angermeier PL, Marchetti MP, Olden J (2016) Predicting invasiveness of species in trade: climate match, trophic guild and fecundity influence establishment and impact of non-native freshwater fishes. Diversity and Distributions 22(2): 148–160. https://doi.org/10.1111/ddi.12391

Hulme PE (2014) Invasive species challenge the global response to emerging diseases. Trends in Parasitology 30(6): 267–270. https://doi.org/10.1016/j.pt.2014.03.005

Jehlik V, Dostalek J, Frantik T (2019) Alien plants in central European river ports. Neobiota, 45: 93–115. https://doi.org/10.3897/neobiota.45.33866

Jeschke JM, Aparicio LG, Haider S, Heger T, Lortie CJ, Pyšek P, Strayer DL (2012) Taxonomic bias and lack of cross-taxonomic studies in invasion biology. Frontiers in Ecology and the Environment 10(7): 349–350. https://doi.org/10.1890/12.WB.016

Keller RP, Drake JM, Lodge DM (2007) Fecundity as a basis for risk assessment of nonindigenous freshwater molluscs. Conservation Biology 21(1): 191–200. https://doi.org/10.1111/j.1523-1739.2006.00563.x

Kosmala M, Wiggins A, Swanson A, Simmons B (2016) Assessing data quality in citizen science. Frontiers in Ecology and the Environment 14(10): 551–560. https://doi.org/10.1002/fee.1436

Langor DW, DeHaas LJ, Foottit RG (2009) Diversity of non-native terrestrial arthropods on woody plants in Canada. Biological Invasions 11(1): 5–19. https://doi.org/10.1007/978-1-4020-9680-8_2

Liebhold AM, Berec L, Brockerhoff EG, Epanchin-Niell RS, Hastings A, Herms DA, Kean JM, McCullough DG, Suckling DM, Tobin PC, Yamanaka T (2016) Eradication of invading insect populations: from concepts to applications. Annual Review of Entomology 61: 335–352. https://doi.org/10.1146/annurev-ento-010715-023809

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3(1): 182–196. https://doi.org/10.1002/ece3.431

Mangiante MJ, Davis AJS, Panlasigui S, Neilson ME, Pfingsten I, Fuller PL, Darling JA (2018) Trends in nonindigenous aquatic species richness in the United States reveal shifting spatial and temporal patterns of species introductions. Aquatic Invasions 13(3): 323–338. https://doi.org/10.3391/ai.2018.13.3.02

Mazza G, Tricarico E, Genovesi P, Gherardi F (2014) Biological invaders are threats to human health: an overview. Ethology Ecology & Evolution 26(2–3): 112–129. https://doi.org/10.1080/03949370.2013.863225

McKinney ML (2001) Effects of human population, area, and time on non-native plant and fish diversity in the United States. Biological Conservation 100: 243–252. https://doi.org/10.1016/S0006-3207(01)00027-1

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14(11): 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Naranjo-García E, Castillo-Rodríguez ZG (2017) First inventory of the introduced and invasive mollusks in Mexico. Nautilus 131(2): 107–126. https://www.biodiversitylibrary.org/item/276658#page/5/mode/1up

Nekola JC, Hutchins BT, Schofield A, Najev B, Perez KE (2019) Caveat consumptor notitia museo: Let the museum data user beware. Global Ecology and Biogeography 28: 1722–1734. https://doi.org/10.1111/geb.12995

Nespolo RF, Bartheld JL, Gonzalez A, Bruning A, Roff DA, Bacigalupe LD, Gaitán-Espitia, JD (2014) The quantitative genetics of physiological and morphological traits in an invasive terrestrial snail: additive vs. non-additive genetic variation. Functional Ecology 28(3): 682–692. https://doi.org/10.1111/1365-2435.12203

Nicolai A, Vernon P, Lenz R, Le Lannic J, Briand V, Charrier M (2013) Well wrapped eggs: effects of egg shell structure on heat resistance and hatchling mass in the invasive land snail *Cornu aspersum*. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology 319(2): 63–73. https://doi.org/10.1002/jez.1767

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52(3): 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution 23(5): 237–244. https://doi.org/10.1016/j.tree.2008.02.002

Robinson DG (1999) Alien invasions: the effects of the global economy on non-marine gastropod introductions into the United States. Malacologia-Philadelphia 41(2): 413–438. https://www.cabdirect.org/cabdirect/abstract/20000806106

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Rubel F, Brugger K, Haslinger K, Auer I (2017) The climate of the European Alps: Shift of very high resolution Köppen-Geiger climate zones 1800–2100. Meteorologische Zeitschrift 26(2): 115–125. https://doi.org/10.1127/metz/2016/0816

Shea EK, Sierwald P, Bieler R, Rosenberg G (2018) Priorities and opportunities for digitizing mollusk collections. American Malacological Bulletin 36(2): 171–177. https://doi.org/10.4003/006.036.0202

Sierwald P, Bieler R, Shea EK, Rosenberg R (2018) Mobilizing mollusks: Status update on mollusk collections in the USA and Canada. American Malacological Bulletin 36(2): 177–215. https://doi.org/10.4003/006.036.0202

Simberloff D (2013) Invasive species: what everyone needs to know. Oxford University Press, Oxford.

Simberloff D, Martin J, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P (2013) Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution 28(1): 58–66. https://doi.org/10.1016/j.tree.2012.07.013

Spear D, Foxcroft LC, Bezuidenhout H, McGeoch MA (2013) Human population density explains alien species richness in protected areas. Biological Conservation 159: 137–147. https://doi.org/10.1016/j.biocon.2012.11.022

Troia MJ, McManamay RA (2016) Filling in the GAPS: evaluating completeness and coverage of open-access biodiversity databases in the United States. Ecology and Evolution 6(14): 4654–4669. https://doi.org/10.1002/ece3.2225

U.S. Congress, Office of Technology Assessment (1993) Harmful Non-Indigenous Species in the United States, OTA-F-565, U.S. Government Printing Office, Washington, 391 pp. https://www.anstaskforce.gov/Documents/OTA_Report_1993.pdf

van Wilgen NJ, Roura-Pascal N, Richardson DM (2009) A quantitative climate-match score for risk-assessment screening of reptile & amphibian introductions. Environmental Management 44: 590–607. https://doi.org/10.1007/s00267-009-9311-y

Vendetti JE, Lee C, LaFollette P (2018) Five new records of introduced terrestrial gastropods in Southern California discovered by citizen science. American Malacological Bulletin 36(2): 232–247. https://doi.org/10.4003/006.036.0204

Vinogradova Y, Pergl J, Essl F, Hejda M, van Kleunen M, Pyšek P (2018) Invasive alien plants of Russia: insights from regional inventories. Biological Invasions 20(8): 1931–1943. https://doi.org/10.1007/s10530-019-02162-y

Yang L, Jin S, Danielson P, Homer C, Gass L, Case A, Costello C, Dewitz J, Fry J, Funk M (2018) A New Generation of the United States National Land Cover Database: Requirements, Research Priorities, Design, and Implementation Strategies. ISPRS Journal of Photogrammetry and Remote Sensing 146: 108–123. https://doi.org/10.1016/j.isprsjprs.2018.09.006

Yeung NW, Hayes KA (2018) Biodiversity and Extinction of Hawaiian Land Snails: How Many Are Left Now and What Must We Do To Conserve Them–A Reply to Solem (1990). Integrative and Comparative Biology 58(6): 1157–1169. https://doi.org/10.1093/icb/icy043

Yesson C, Brewer PW, Sutton T, Caithness N, Pahwa JS, Burgess MW, Gray WA, White RJ, Jones AC, Bisby FA, Culham A (2007) How global is the global biodiversity information facility? PloS ONE 2(11): e1124. https://doi.org/10.1371/journal.pone.0001124

Supplementary material 1

All records with associated georeferences used in analyses

Authors: Nicholas S. Gladstone, Trystan A. Bordeau, Christy Leppanen, Michael L. McKinney

Data type: Geospatial

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.57.52195.suppl1